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GETTING BIGGER FASTER: MEDIATION OF SIZE-SPECIFIC MORTALITY VIA FUSION IN JUVENILE CORAL TRANSPLANTS

LAURIE J. RAYMUNDO[1,3] AND AILEEN P. MAYPA[2,4]

[1]*Silliman University Marine Laboratory, Dumaguete City 6200, Philippines*
[2]*Project Seahorse Foundation for Marine Conservation, Inc., 12 Espina Village I, B. Rodriguez Street, Cebu City 6000, Philippines*

Abstract. Size-specific mortality can determine whether coral transplants become successfully established in a reef rehabilitation effort. Presented here are results of a study of size-specific mortality in laboratory-cultured transplants, and the mediating effect of fusion on their survival and growth. Culturing seeded colonies for transplantation minimizes impacts to source reefs. This strategy provides an opportunity to enhance survival of a transplanted population by incorporating selected aspects of colonial modular biology, such as fusion, into the culture phase. Despite efforts to develop a completely field-based method, settlement and early survival of juveniles of the scleractinian *Pocillopora damicornis* were much higher in laboratory aquaria than among those settled on reef substrate, highlighting the difficulty of direct seeding and justifying the higher effort involved in laboratory rearing.

Juvenile colonies from four size cohorts (≤3 mm, 3.1–6 mm, 6.1–10 mm, and 10.1–29 mm), outplanted to a reef in August 1997, showed one-year survival of 0%, 2.5%, 16.3%, and 47.5%, respectively, illustrating significant size-specific mortality. Colony fusion resulted in lower 6-mo mortality (unfused colonies: 34.5% ± 0.4%, fused pairs: 14.0% ± 2.5%, fused groups: 8.3% ± 4.8%; means ± 1 SE), and chimeras of >2 fused colonies produced polyps faster. Tissue necrosis along fusing colony borders was observed between 8-mo-old colonies. This suggested a rejection response, though colonies fusing prior to this age remained stable for up to one year. A transition matrix revealed that fused colonies showed greater probability of growth to the next size class, while unfused colonies showed higher mortality and stasis. Growth trajectories based on transition probabilities suggested that fused colonies would reach reproductive size much earlier than unfused colonies. To test the hypothesis that larvae aggregatively settle to increase their chances of fusing, settlement patterns were determined in larvae of same- vs. mixed-parent groups. Settled larvae were aggregatively distributed, with no difference in aggregation strength in larvae of same- vs. mixed-parent groups. Results suggest a benefit of fusion to survival and growth within the first eight months in juvenile coral colonies. Fusion could be used as a strategy to obtain larger colonies faster, provided they remain stable over time. Laboratory seeding and rearing of juveniles to 10 mm provides a workable alternative to fragment transplantation in brooding coral species, and similar strategies may also be developed for spawning species.

Key words: *coral culture; coral transplant survival and growth; fusion, corals; mortality, size-specific;* Pocillopora damicornis; *reef rehabilitation; scleractinian; transition matrix.*

INTRODUCTION

In colonial organisms such as coral, size is considered the most accurate determinant of mortality rate and reproductive output (Connell 1973, Hughes and Jackson 1980, Rylaarsdam 1983, Hughes and Connell 1987). Because the modular construction of corals allows fusion, fission, and partial mortality, age is often decoupled from size and cannot be used to predict changes in the demography of a population (Hughes and Connell 1987). Two consequences of this strategy affect the rate at which corals can become reestablished on degraded reefs. First, corals, like many marine invertebrates, display Type III survivorship, with highest mortality among the smallest size classes (Deevey 1947). The growth rate of highly vulnerable juveniles determines the length of time to reach a size refuge, thereby influencing early mortality and recruitment. Second, sexual reproduction in many corals requires a minimum colony size for gamete production (Harrigan 1972, Rinkevich and Loya 1979, Kojis and Quinn 1984, Szmant-Froelich 1985, Chornesky and Peters 1987). Fragmentation of sexually reproductive colonies, therefore, may cause a reversion to a pre-reproductive state (Zakai et al. 2000). Likewise, colonies grown from seeded larvae must grow to reach reproductive size before they can contribute to recruitment. Understanding the consequences of size on coral growth and es-

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[3] E-mail: lauriejr@dgte.mozcom.com

[4] Present address: Silliman University Marine Laboratory, Dumaguete City 6200, Philippines.

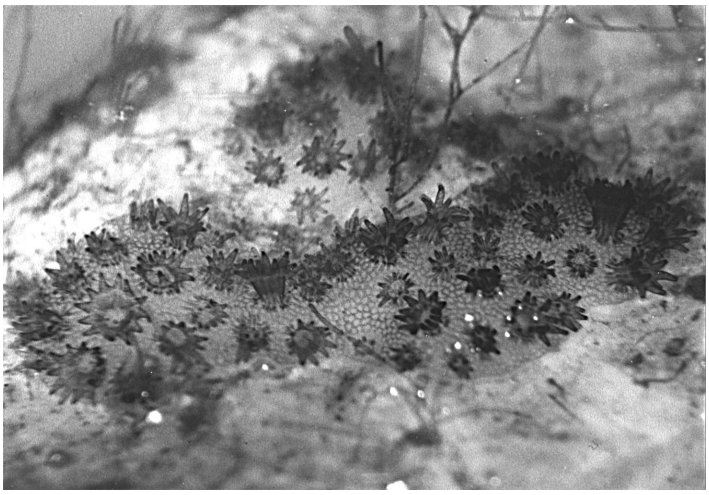

PLATE 1. Fusion between three juveniles, showing new polyps around colony margin. The three large polyps in the center of the colony are the original metamorphosed larvae that settled in close proximity to each other. Photo credit: Laurie Raymundo.

tablishment can guide the development of approaches for the optimal use of juvenile colonies or fragments for reef rehabilitation.

Establishing a viable, persistent coral community is the major goal in reef rehabilitation (Rinkevich 1995). The most widely used approach is coral transplantation, using small fragments or whole colonies (Maragos 1974, Alcala et al. 1982, Harriot and Fisk 1987, Yap et al. 1992, Clark and Edwards 1995, Nagelkerken et al. 2000), but issues such as size-specific survival and growth and the consequences of fragmentation on donor colonies of the transplanted species are rarely considered. Corals grow indeterminately with little evidence of reproductive output decline with aging, though they suffer high pre-reproductive, size-specific mortality. In addition, colony recovery from stress or injury may be size related, as energy may be translocated within a colony for tissue repair. Therefore, larger colonies have greater energy reserves and may recover faster, though with a corresponding reduction in reproductive output (Oren et al. 2001). These issues have not been addressed in the rehabilitation literature, though their investigation could lead to greater success in reestablishing viable populations.

Concern over the damage caused to donor reefs by removing large numbers of fragments has triggered exploration into other sources of transplantable coral. Coral seeding—settling planula larvae onto appropriate substrates—is one alternative. Though growth to adult sizes from settled larvae takes longer than it would using fragments, this approach has numerous advantages: (1) large numbers of planulae are obtainable from a single colony and many brooding species release larvae for several, if not all, months of the year, (2) collection of larvae does not necessitate permanent damage to, or removal of, donor colonies, and (3) colonies reared from larvae have greater genetic diversity than those grown from clonal fragments because they are sexually produced. Direct seeding of larvae onto reef substrate has been used by P. W. Sammarco, D. A. Brazeau, and T. N. Lee (*unpublished manuscript*) with limited success and high mortality. An approach that increases early survival of seeded colonies, such as the incorporation of a laboratory-rearing phase, could provide a viable alternative to fragment transplantation.

Survival of juvenile colonies can potentially be increased by promoting fusion to increase colony size faster (see Plate 1). Colonies that get larger faster would be predicted to reach a reproductive size faster. Fusion occurs in the wild in many sessile invertebrates that contact each other as a result of growth (Buss 1982, Rinkevich and Weissman 1987). Whether the benefits of fusion outweigh the negative consequences is the subject of much debate. Beneficial consequences are larger colonies with higher growth, better competitive ability, lower mortality, and greater genetic variability (Hughes and Jackson 1980, Grosberg and Quinn 1986, Lang and Chornesky 1990, Chadwick-Furman and Weissman 1995). Resorption (a dominant genotype absorbs the tissues of a subordinate) and somatic and/or germ-cell parasitism (the subordinate genotype remains within the colony as totipotent stem cells that then parasitize the dominant colony; Buss 1982, Rinkevich and Weissman 1992, Pancer et al. 1995) are negative consequences. Transient fusion may represent a temporary mechanism for immediately increasing size without the negative consequences (Grosberg et al. 1996, Frank et al. 1997). However, fusion outcomes are not always so clear-cut. Maldonado (1998) found that while fusion resulted in larger colonies of the sponge *Tedania ignis*, the larger size did not confer a survival advantage. Resorption in the ascidian *Botryllus schlosseri* was common in chimeras composed of two genotypes, but rare in those with more than two genotypes (Rinkevich 1996). In laboratory vs. field assays, resorption and slower growth were common in laboratory-reared *Botryllus* colonies but rare in those grown in the field, though chimeras showed lower fe-

cundity than unfused colonies in field assays (Chadwick-Furman and Weissman 1995, 2003). The authors speculated that lower fecundity was a consequence of competition between genotypes within the chimera. Fusing with close kin can reduce the risk of such negative consequences (Buss 1982, Grosberg and Quinn 1986), especially in multi-genotype chimeras (Rinkevich 1996). Aggregative settlement of close kin may facilitate such interactions and prevent competition between unrelated colonies (Grosberg and Quinn 1986). However, this requires larvae with precise allorecognition ability, such as has been documented in ascidians (Scofield et al. 1982) but is less understood in lower invertebrates. Limited evidence suggests that corals require a maturation period during which they have little or no ability to distinguish between varying levels of relatedness. In the coral *Stylophora pistillata*, this process takes four months, after which fusion no longer occurs between genetically distinct genotypes (Frank et al. 1997). The above evidence highlights the need for further elucidation of the evolutionary role of fusion and its consequences, particularly in the context of its use as a potential tool in culturing colonial invertebrates.

This paper reports a study to evaluate the feasibility of coral seeding as a rehabilitation alternative and to investigate the role of fusion in mediating size-related growth and mortality in seeded colonies. We predicted that laboratory seeding and rearing would result in higher survival than field seeding, but the ease with which field seeding could be accomplished would outweigh the lower survival. To determine the most appropriate size at which to transplant laboratory-reared colonies, we tested the hypothesis that significant size-related mortality among transplants would result in low establishment of very small colonies, while larger ones would survive to reproductive size. Finally, to investigate an approach to achieving a larger size faster, we quantified the long-term effects of fusion between conspecific juvenile colonies on growth and survival. We predicted that fusion between neighbors would result in significantly greater growth and survival. In addition, we predicted that larvae would aggregatively settle to increase the probability of fusion and that aggregation would be stronger among related larvae than among unrelated larvae, to reduce the potential negative consequences of fusion.

Materials and Methods

Spawning and larvae collection

This study was conducted at the Silliman University Marine Laboratory (SUML) and Bantayan reef, central Philippines, from January 1997 to August 1999. Bantayan reef is immediately offshore of SUML, and provides a readily accessible study site. *Pocillopora damicornis* Linnaeus was used as a study species; it is ubiquitious and easily reared in aquaria. *P. damicornis* is a brooding species; fertilization and embryonic development occur internally and zooxanthellate larvae are competent to settle within one to two days upon their release (Richmond 1997). Although this species is known to have two morphs that differ in their spawning timing in other areas of the Pacific (Richmond and Jokiel 1984), there was no evidence for the existence of more than one morph in the Bantayan population and colonies consistently spawned monthly for seven nights immediately after new moon (Raymundo et al. 1997). Colonies were obtained from the reef two days prior to spawning and kept in laboratory aquaria for collection of larvae. Although Rinkevich (1995) successfully obtained larvae without removing colonies from the reef, our attempts at this were unsuccessful; plankton mesh bags placed over the colonies at sunset yielded very few larvae the next morning. It was more efficient to bring spawners into laboratory aquaria for larvae collection. Each night during spawning, they were placed in individual buckets of fresh-flowing seawater and larvae were collected into nitex mesh cups (125-μm mesh size) when they floated to the surface. Larvae were counted the following morning by 0800 hours. Spent spawners were returned to the reef and cemented in place using Pioneer marine epoxy. Field settlement studies were conducted on Bantayan reef and fusion and settlement studies were conducted in rearing tanks at SUML.

Larval settlement and early mortality

To address the hypothesis that early laboratory rearing results in higher survival of juveniles, we measured settlement success in laboratory rearing tanks vs. on reef substrate and monitored post-settlement mortality in these environments. To determine settlement success in laboratory tanks, spawned larvae were stocked in bowls of fresh seawater at a density of 20 larvae/500 mL the morning after their release, after methods developed by R. H. Richmond (*personal communication*). Five parent colonies were used for each of nine spawning periods, from February 1997 to August 1998 (see Table 1). Planulae from each colony were settled separately, so each settlement bowl contained larvae assumed to be either half-sibs or full-sibs. The number of replicate bowls per spawning colony was dependent on the number of larvae spawned per parent. Each bowl was supplied with four pieces of roughened marine-limestone commercial tiles averaging 48 cm^2, conditioned in seawater for two weeks to develop a bacterial/algal film. Total available surface area per bowl averaged 190 cm^2. Planulae were given 24 h to settle, and successful settlement was determined the next morning as the number of permanently attached and metamorphosed primary polyps on the tiles. A percentage of successfully settled vs. stocked larvae was calculated per bowl and per parent colony using the formula (number of settled juveniles)/(number of stocked larvae) $\times$ 100.

Tiles with settled primary polyps were transferred to shaded laboratory culture tanks (1.5 × 0.75 × 0.75 m) with flowing unfiltered seawater and aeration. Tanks were partially shaded with mesh to avoid overheating and overexposure to direct sunlight, to approximate light levels at depths at which adult colonies grew on the reef. Seawater was pumped into the laboratory from Bantayan reef, close to where the field settlement trials were run. This ensured that water quality for rearing in laboratory tanks and reef environments were identical, though it was assumed that water temperatures on the reef fluctuated less than those in laboratory rearing tanks. Temperature in the tanks ranged on average daily from 24°C to 30°C, and salinity was constant at 35‰. Supplementary feeding was not given, as it was assumed that the unfiltered seawater would supply the nutritional needs of the growing colonies. Mortality was censused daily for one week, and weekly thereafter for one month.

Settlement success on reef substrate was determined by settling larvae from the same parents simultaneously with those settled in the laboratory during selected months (a subset of three out of the five parent spawners with the highest planula numbers were used each month). Prior to spawning, patches of bare reef rock at 4-m depth were prepared by removing all macroalgae and sand. Settlement traps were affixed to the substrate with epoxy to prevent larvae from dispersing. Traps consisted of inverted 600 mL clear plastic screw-top jars, with the bottoms removed and covered with 125-μm nitex mesh net, to allow for water exchange. A hole with a removable plug allowed planulae to be injected into the trap. The top of the jar was cut out, and the rim was sealed to the substrate with epoxy. Substrate surface area available for settlement was 160 cm^2, including the sides of the jar affixed to the substrate where many of the larvae settled. Planulae were haphazardly collected from each parent and carefully placed into sterile syringes filled with fresh seawater using a pipette (n = 50 larvae per 50-mL syringe; each syringe contained larvae from a single parent). The syringes were kept in a water bath for transport to the reef for no more than one hour. Larvae were then gently injected into settlement traps at densities of 50 larvae/trap. A previous trial run indicated low settlement, so stocking density was higher than that in laboratory trials, to increase the probability of settlement. Continual fresh seawater circulation within the traps ensured water quality would not decline with the higher stocking density. All larvae appeared viable and competent when they were introduced into the trap. Settlement was censused 24 h later and the seeding trap was removed. Due to high mortality during the first three trials, traps large holes in the side placed over juvenile colonies for one month, for the last three trials. These traps allowed free water exchange, but prevented access by grazers and minimized siltation. Mortality was censused daily for one week, and weekly thereafter for one month. There were a number of confounding factors that complicated a comparison of results in laboratory vs. field assays; specifically, larval stocking density differed due to the low settlement success in trial field assays (20 larvae per bowl vs. 50 larvae per trap) and settlement surface area differed slightly between the two (190 cm^2 per bowl vs. 160 cm^2 per trap) as did the physical conditions of the microhabitat, such as water movement and daily temperature variation. However, these limitations were difficult to avoid, and attempts were made to standardize the results.

Settlement and early mortality in laboratory vs. field trials were each compared using one-way ANOVA, with each month considered a replicate (n = 5 mo). Treatment comparisons were pooled across sibships for the five trials to obtain a sufficient sample size, as settlement was very low in the field. The effects of both treatment (laboratory vs. field) and larval source (parent) on settlement success and first-week mortality were examined using a two-way ANOVA for the two months (March 1998 and July 1998; Table 1) for which cages were used, as sufficient data points were available. This allowed an examination of an interaction between parent and treatment. Settlement and mortality in laboratory trials (n = 6 replicate months) were tested against planula source (i.e., parent) to test for between-parent differences in larval success using one-way ANOVA, with n = 9 replicate months.

To establish a baseline growth rate of laboratory-settled and laboratory-reared juveniles, a subset of 20 colonies were haphazardly selected from the February 1997 cohort for regular monitoring. Maximum colony diameter, and diameter perpendicular to maximum were measured weekly for six months using calipers. Surface area and mean weekly growth rates were calculated from diameter measurements. Data were then analyzed using repeated-measures ANOVA, testing weekly increase in surface area against colony size over six months, to determine if growth rate altered with increasing colony size.

Size-related mortality

To quantify the effect of size at transplantation on subsequent survival and growth in the field, four groups of juvenile colonies (from February, April, June, and July 1997 cohorts) were reared in laboratory culture tanks from larvae spawned and settled using the procedure described above. All colonies used in this experiment were grown from single planulae. In August 1997, 320 colonies were assigned to four size classes: ≤3.0 mm maximum diam.; 3.1–6 mm; 6.1–10 mm; and 10.1–29 mm, roughly corresponding to 1 mo, 3 mo, 5 mo, and 6 mo of age. Substrate tiles (n = 320 tiles), each with a single colony, were transplanted to three replicate patches of reef rock at 4-m depth on Bantayan reef and cemented in place using marine epoxy. Care was taken to prevent direct contact between living tissue and epoxy. Subsequent survival and growth of

transplants were monitored for one year. Growth was determined by measuring colony maximum diameter. The original intention was to analyze growth data with repeated-measures ANOVA, which would have allowed an analysis of the effect of increasing size on growth rate and survival. However, tags identifying individual colonies were often damaged or overgrown, so it was impossible to identify individual colonies during successive samplings. Therefore, growth data were pooled across size class during each sampling, and means and standard deviations were calculated. This was possible because tags were color coded for each size class and numbered for each colony. So in cases where the numbers were overgrown or damaged, the colony could still be identified as to original size class by tag color. Survival data were analyzed using Cox proportional-hazards analysis (SAS Institute 1994). This test analyzed size at transplantation as a factor determining later fate, with fate defined as either mortality within discrete time intervals (defined as the periods between censusing) or survival to the end of the monitoring period.

To determine if surviving transplants had grown to reproductive size, three of the largest colonies were haphazardly selected and brought into the laboratory in July 1999, prior to spawning. Colonies ranged from 6.7 cm to 7.3 cm in diameter, and were ~2.5 yr old. They were held in spawning vessels following the previously described protocol. The presence of planulae the next morning indicated a reproductive colony. Colonies were then returned to the reef and reattached.

Fusion effects on survival and growth in laboratory conditions

The effects of fusion between sibling juveniles on their survival and growth were investigated to test the prediction that fusion between adjacent kin would result in both faster growth and higher survival than colonies growing from single larvae. As all parent colonies belonged to a single morphology, juvenile colonies that fused formed an apparently unified single colony wherein the original genotypes were indistinguishable. When upward growth began to appear (at approximately five months of age), a single branch developed in the center of the colony, rather than multiple branches from each genotype. Therefore, each chimera was treated as an independent replicate. In July 1998, larvae from three parent colonies were stocked at a density of 60 larvae/500 mL, using the protocol described above (see *Larval settlement*. . .). The higher density increased the probability of larvae settling in close proximity and later fusing. Three replicates (180 larvae total) from each parent were set up. Settlement and fusion at 24 h were censused the next day, and tiles containing settled juveniles were transferred to rearing tanks ($n = 3$) with separate water supplies and aeration, to be reared under the same environmental conditions described above (see *Larval settlement*. . .). Tiles from the three parents were haphazardly assigned to each rearing tank, so that each tank held similar numbers of colonies from both individual and fused juveniles from each parent. Neighboring colonies were subsequently allowed to fuse as they grew in contact with each other over the 12-mo monitoring period. Survival, growth, fusion rate, and size of fused groups were monitored weekly for 6 mo, then every 2 wk for another 6 mo. All fused colonies, and a subset of 40 haphazardly selected individual colonies, were monitored for growth. To avoid tissue injury around the colony boundary due to caliper use, growth was measured by counting the number of polyps per colony for the first 6 mo. Starting at four months, caliper measurements were taken as well as polyp counts. Accurate polyp counts became increasingly difficult as colonies developed upward growth and branched, and were abandoned by six months. Growth rate, therefore, was defined as the increase in the number of polyps per week from zero to 6 mo of age, and increase in colony maximum diameter from 4 mo to 12 mo of age.

Data were analyzed by comparing the fate and growth of colonies in three groups differing in fused status: individuals (IC) = colonies growing from a single larva, fused pairs (FP) = colonies that had fused with one other colony, and fused groups (FG) = colonies that had multiple fusions with two or more others. Fused-group size ranged from three to ten. Growth data were normalized using a Box-Cox transformation (Velleman 1997; transformation factor = 0.333). The effects of group size (IC, FP, FG), parent (i.e., planula source; $n = 3$ parents), and rearing tank ($n = 3$ tanks) on the slopes of the growth-rate curves over six months were tested using ANCOVA. Because of the small number of colonies in the FP and FG populations, an analysis of the effect of colony size on growth rate could not be accomplished for the entire population. In addition, transitions between the groups throughout sampling (i.e., individuals fused, fused pairs became triplets, etc.) further reduced sample size in the FP and FG populations. Mortality in the three groups was analyzed using logistic regression, testing for the fate (alive or dead) of colonies at the end of 6 mo, using group size, parent, and rearing tank as predictors.

Transition tables were developed based on rates of transition between size classes over 6 mo for unfused vs. fused colonies. These allowed size-specific integration of the rates at which colony size and mortality changed depending on whether or not a colony fused (Harvell et al. 1990). Size classes were formulated based on ranges that encompassed the mean polyp number at bimonthly census intervals for all colonies in the cohort (smallest size class: 3–5 polyps; largest size class: 45–65 polyps). Possible transitions, or fates, within each size class included growth to the next size class, shrinkage, stasis (remaining within a size class), or death, and were ordered according the number of colonies experiencing each fate at 6 mo of age. Data

were examined using ordinal logistic regression, a modification of the approach used by Harvell et al. (1990). Fused state and size class were used as predictors of colony fate for the overall model. An iterative regression was used to determine how fusion was specifically affecting colony fate. Data per fate and fused state were pooled across size classes to represent the total number of colonies showing a specific fate. This was necessary because some colonies had the same fate more than once (i.e., growth at each size class; stasis or shrinkage at more than one size class). These pooled data were then tested per fate separately, using fused state as a predictor. Data points with nonsignificant differences in fate were removed from subsequent tests. Size class was treated as a continuous variable due to the lack of data points in the largest size class for unfused colonies.

Settlement patterns

Settlement patterns in *Pocillopora damicornis* were examined to address the hypothesis that larvae settle aggregatively, resulting in a greater probability of fusing. Further, if larvae prefer settling with kin, as shown by Grosberg and Quinn (1986) for ascidians and Keough (1984) for bryozoans, they would be predicted to aggregate more strongly in single-parent groups than in mixed-parent groups. In July 1999, 30 donor colonies were collected from Bantayan reef; donors collected were at least 10 m apart to minimize relatedness (Potts 1976, Keough 1984). Following methods of Keough (1984) and Young and Braithwaite (1980), we settled larvae from single-parent and mixed stocks at densities of 30 larvae/500 mL. This density was chosen because the settlement surface was slightly larger than that previously used with densities of 20 larvae/500 mL. Thus, aggregation would not be an artifact of overcrowding, but density was high enough to ensure an adequate sample size. *P. damicornis* planulae, like many other invertebrate larvae, use chemical cues on the substrate to select favorable settlement sites, often taking several hours to choose an attachment position (L. J. Raymundo, *personal observation*). Therefore, at the densities at which the larvae were stocked, it is likely that they came into contact with other larvae during this extended searching period. For single-parent groups, larvae were collected from eight parents. Three to five bowls of larvae were settled for each of the eight parents, for a total of 30 single-parent bowls. For mixed-parent groups, three larvae were collected from each of 10 parents (the eight mentioned above plus two more) and stocked in a mixed-parent bowl. Thus, there was a 10% chance of a larva settling next to kin in this bowl. This set-up was replicated 30 times and run simultaneously with the single-parent bowls. A smoked-glass plate, 8 cm $\times$ 11 cm $\times$ 2 mm, was placed into each bowl after being roughened with sandpaper and conditioned in seawater. By providing optimum conditions on a single homogeneous surface, we assumed that settlement position was determined primarily by proximity to other spat, rather than a preferred microhabitat choice.

Larvae were allowed 24 h to settle, after which maps were made of the position of all metamorphosed spat settled on each glass plate. Distance between each spat and its nearest neighbor was measured from these maps using a caliper and these distances were analyzed using nearest-neighbor analysis, as presented in Clark and Evans (1954). This method was employed by Grosberg and Quinn (1986), using a model with multiple trials similar to the multiple settlement plates used in this study; it is straightforward to use and interpret and does not require that a subset of data points be used. This was an important consideration, as sample size per plate was small, varying between 12 and 26 spat. Larvae settling within a 0.5-cm distance from the edge and those settled on upper surfaces were not used in calculations. This eliminated bias due to edge effects and differences in the microenvironment between upper and lower surfaces. The degree of randomness, R, was calculated per plate using the formula

$$R = \frac{r_A}{r_E} \tag{1}$$

where

$$r_A = \frac{\sum r}{N} \qquad r_E = \frac{1}{2\sqrt{\rho}}$$

and r_A = actual dispersion on settlement plate, r_E = expected random dispersion, ρ = spat density/plate, N = number of spat per plate, and r = distance between neighbors. Difference in aggregation strength between larvae of mixed vs. same parents was tested with one-way ANOVA using R values for each plate. The test of significance for degree of aggregation used the formula

$$c = \frac{r_A - r_E}{\sigma r_E}.$$

These c values, calculated per plate, were compared to the value $Z = 1.96$ from the normal distribution table for a two-tailed test at $\alpha = 0.05$ (Clark and Evans 1954).

Results

Larval settlement and early mortality

Table 1 summarizes settlement success and early mortality in laboratory aquaria vs. reef substrate for successive trials over a 2-yr period. Settlement was consistently higher in laboratory aquaria than on reef substrate (ANOVA, df = 1, 8, $F = 7.09$, $P = 0.0207$) and first-week mortality, lower in the laboratory than in the field (ANOVA, df = 1, 8, $F = 6.972$, $P = 0.0230$). As larvae were handled similarly in both laboratory and field trials and settled in water from the same source, it is doubtful that transplantation stress

TABLE 1. Settlement success and post-settlement mortality in coral spat reared in laboratory vs. field-seeding trials at Bantayan Reef, Philippines.

	Laboratory tanks			Reef substrate		
Date	No. larvae stocked	Settlement success (%)	Mortality at 1 wk (%)	No. larvae stocked†	Settlement success (%)	Mortality at 1 wk (%)
1997						
February	682	48.1 ± 6.0	21.7 ± 4.7	…	…	…
April	500	70.8 ± 4.7	20.5 ± 13.9	…	…	…
June	510	72.1 ± 1.2	35.5 ± 4.3	300 (6)	21.2 ± 7.3	87.6 ± 15.2
July	662	60.4 ± 3.0	12.3 ± 2.4	…	…	…
October	360	16.7 ± 2.2	37.6 ± 12.8	300 (6)	10.0 ± 7.5	100
1998						
February	960	67.0 ± 4.6	34.4 ± 7.2	…	…	…
March	1500‡	67.0 ± 0.8	25.6 ± 25.2	450 (9)	15.4 ± 10.1	42.1 ± 40.9
July	540	70.0 ± 1.7	7.1 ± 6.6	540 (9)	9.4 ± 11.8	26.0 ± 27.7
August	360	62.2 ± 10.8	not censused	480 (12)	6.0 ± 10.9	32.9 ± 41.9
Mean ± 1 SD	…	59.4 ± 17.6	24.3 ± 11.1	…	12.4 ± 6.1	57.7 ± 33.7

Notes: Five parent spawners were used per month, and results are pooled across larvae from different parents. There were three tanks in the laboratory. Data are means ± 1 SD.

† The number in parentheses is the number of traps stocked.

‡ Starting in March 1998, settled spat were enclosed in rearing cages on the reef immediately after settlement was censused. The cages were cleaned weekly and left in place for one month.

can account for this large difference. In addition, site preparation on the reef ensured that the substrate settlement surfaces were almost identical in terms of composition ($CaCO_3$ rock) and conditioning (natural bacterial/algal film). The addition of protective traps lowered mortality from predation or grazing, but not significantly. Mortality in the field was still significantly higher than that in the laboratory (ANOVA, $F = 9.714$, df = 1, 3, $P = 0.0036$) and settlement success lower (ANOVA, $F = 188.46$, df = 1, 4, $P < 0.0001$) for the two months for which the cages were used (Table 1: March and July 1998). In addition, larval source (i.e., parent) had an effect on settlement (ANOVA, $F = 3.09$, df = 1, 16, $P = 0.02$); a single parent produced larvae that settled significantly less than all others in both laboratory and field trials (Parent no. 37; Bonferroni post hoc $P = 0.016$). Larval source had no significant effect on post-settlement mortality. Interactions between laboratory vs. field treatment and parent were also not significant, nor was sampling month. In addition, the high algal growth and sand accumulation in the traps required continual weekly maintenance, making them impractical for extended use.

Settlement success differed between laboratory-reared larvae from different parents ($n = 14$ parent colonies; 180–240 planulae per parent), though the significance was also due to a single colony that produced larvae that remained competent but did not settle within the 24-h period (ANOVA, $F = 7.0476$, df = 13, 104, $P \leq 0.0001$; Bonferroni post hoc test: colony no. 20 $\ll$ all other colonies; $P < 0.0004$). Likewise, post-settlement mortality also differed significantly (ANOVA, $F = 2.8769$, df = 13, 104, $P = 0.0023$), again due to larvae from a single parent that survived less than all others (Bonferroni post hoc test: colony no. 13 $\gg$ all other colonies; $P = 0.026$).

Juveniles grew an average of 2.26 ± 0.46 mm per wk (mean ± 1 SE) under laboratory conditions. Growth rate varied significantly over the 6-mo of monitoring (repeated-measures ANOVA, $F = 1816$, df = 29, 667, $P < 0.0001$), increasing as colonies grew larger. Colony surface area significantly affected growth rate over time (surface area × repeat interaction, $F = 1.664$, df = 29, 667, $P = 0.004$).

Size-related mortality

Juvenile colonies at least 10 mm in diameter when transplanted showed the highest successful establishment (Fig. 1). Survival to one year was significantly different between the four size cohorts (Cox risk ratio = 0.84825, $P < 0.0001$), indicating strong size-specific differences in mortality. No colonies from the smallest size class survived to one year and only 2 out of 80 colonies from the second smallest survived. Survival of the third size class was higher still, though lower than that of the largest size. Growth data suggest that growth rates in the field were slower those that in the laboratory; colonies in the third size class at 16 mo old (12 mo post-transplant) were the same size as colonies from the largest size class at 12 mo old (6 mo post-transplant; Fig. 1). Colony shrinkage was high shortly after transplantation, but declined to almost zero by the third month. Larger colonies displayed this response more than smaller colonies; the 6-wk census revealed that none of the smallest size class had shrunk, while 18.8% of survivors in the second size class, 29.3% of the third size class, and 33.3% of the largest size class had smaller colony diameters. By three months, no colonies in the two smaller classes, only one (3.3%) in the third class, and six (10.9%) in the largest class displayed smaller diameters than those from the previous sampling period.

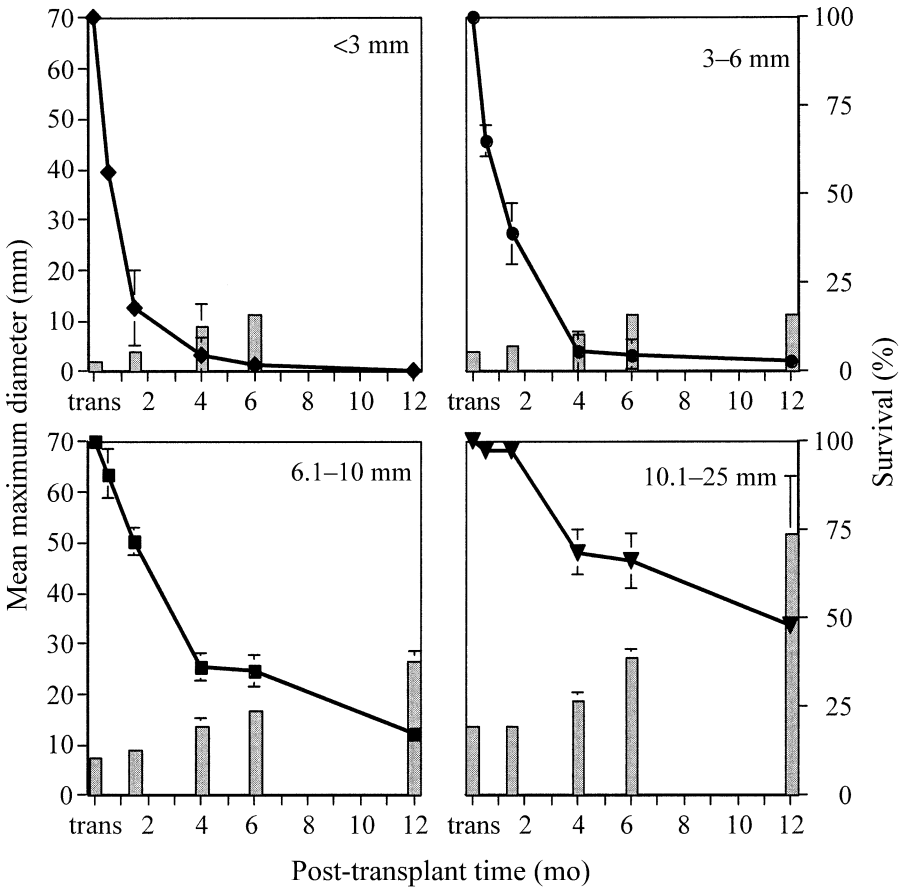

FIG. 1. Survival and growth of juvenile *Pocillopora damicornis* colonies transplanted in four size cohorts ($n = 80$ colonies per cohort, $n = 3$ recipient sites). The size reported in the upper right corner of each panel is size class at transplantation. Data are means ± 1 SE; shaded bars indicate mean maximum diameter; and lines indicate percentage survival per size class.

The 1-yr census revealed 23 new *P. damicornis* recruits in the immediate vicinity of the transplantation site, suggesting recruitment from the transplants. These new colonies were between 9 mm and 11 mm in diameter; approximately four to six months old. Spawning by surviving transplants was verified in August 1999 by the presence of planulae from the colonies during spawning, though the source of the new recruits could not be verified.

Fusion effects on survival and growth in laboratory conditions

Settlement in high density (60 larvae/ 500 mL) resulted in higher rates of fusion than had been observed with lower densities. The 24-h settlement census of the July 1998 cohort yielded 325 individuals, 22 fused pairs, and 3 triplets. Fusion was allowed to continue throughout the 12-mo monitoring period as colonies grew into contact, and no signs of rejection or chimera instability appeared until ~8 mo post-settlement. At this age, tissue became necrotic and algae colonized along the margins between colonies fusing just prior to eight months and thereafter. A total of eight such rejection responses were observed between eight and nine months, several of them between previously formed chimeras. Thus, colonies always fused and remained stable prior to eight months of age, while those contacting a neighbor at eight months or later showed rejection of this new contact. Fusion rate was a function of growth rate and distance between colonies (most colonies that fused settled within several millimeters of each other), and independent of genotype.

Growth rates, measured in polyp production per colony, are presented in Fig. 2. Mean growth rate over six months was significantly different among the three group sizes (Table 2), though the largest difference existed between fused groups and the other two. An exponential curve provided the best fit for the growth-rate data (Fig. 2), which is predicted from an iterative growth strategy whereby each new polyp gives rise to several more. There were no differences in weekly polyp production between fused pairs (1.0 ± 0.1 polyps/wk [mean ± 1 SE]) and individual unfused colonies (0.7 ± 0.1 polyps/wk), but colonies which had fused into larger chimeras (from 3–10 original larvae) produced more polyps per week (2.1 ± 0.4 polyps/wk;

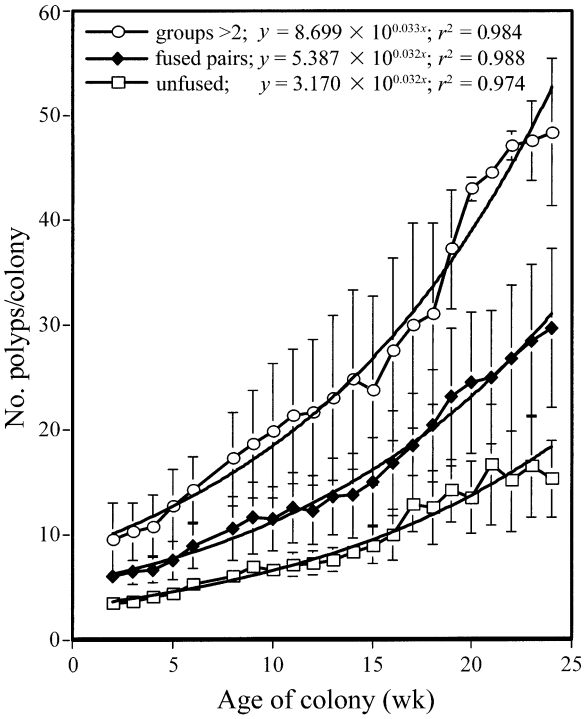

FIG. 2. Growth rate of fused vs. unfused juvenile colonies of *Pocillopora damicornis* reared in laboratory tanks. Data are means ± 1 SE; $n = 3$ rearing tanks. Means per tank are based on 34 individuals (unfused, IC), 40 fused pairs of colonies (FP), and 9 fused groups of >2 colonies (FG).

ANOVA, df = 2, 46, $F = 8.3487$, $P = 0.0009$, post hoc $P = 0.00117$). However, polyp production did not differ significantly between weeks as colonies grew older and larger (ANOVA, df = 20, 1812, $F = 1.0602$, $P = 0.423$). Slopes of the regression lines of the three groups were not significantly different (Table 2: fused state × age interaction). Both parent and tank effects were significant; one parent produced juveniles that grew significantly faster than those from the other two parents (Table 2). A tank effect was suspected during the fourth month of sampling, when shrinkage and colony bleaching were noticed in the third rearing tank. This period corresponded with the 1997–1998 El Niño Southern Oscillation bleaching event. We observed that this tank received greater sunlight in the afternoon than did the other two, which may not have resulted in noticeable colony stress until ambient water temperatures increased. The problem was corrected with additional shading, but colonies in this tank grew significantly slower prior to additional shading (Table 2). However, colonies from all parents and of all group sizes were distributed approximately equally among the three tanks, so it is unlikely that the differences in growth and survival consistently observed among the three group sizes were due to either the parent or the tank effect.

Six-month mortality among groups is presented in Fig. 3. Survival of colonies developing from single planulae was significantly less than the fused pairs and groups throughout the 6-mo period (Table 3; 1.8% ± 0.3% weekly mortality; [mean ± 1 SE]). Colonies derived from the largest number of fused planulae survived the best, though differences between fused pairs (0.2% ± 0.1% weekly mortality) and groups (0.1% ± 0.03% weekly mortality) were not significant. Mortality rate showed a characteristic steady decline over time with increasing age/size until 4 mo. This correlated with the start of the period of increased illumination and water temperature in the third rearing tank, as well as the ENSO bleaching event. In addition, both parent and rearing-tank effects were significant (Table 3), likely for similar reasons as those stated above affecting growth rate.

Transition probabilities between size classes for unfused and fused colonies are represented in Fig. 4. Mortality in both groups was limited to the two smallest size classes. More fused colonies consistently moved to the next size class than did unfused colonies, and no unfused colonies attained the largest size class at 6 mo. Chimeras also showed lower mortality. Over time, the number of unfused colonies remaining within a size class (stasis) increased, while stasis was lower and re-

TABLE 2. Results from ANCOVA of fused state, age, rearing tank, and parent on weekly polyp number in juvenile colonies of the scleractinian coral *Pocillopora damicornis*.

Factor	df	*F*	*P*	Bonferroni post hoc test	
				Results	*P*
Age (mo)	5	116.2	≤0.0001	6 = 5 > 4 > 3 = 2 > 1	<0.05
Fused state, FsSt	2	73.6	≤0.0001	FG > FP > IC	<0.05
Tank	2	23.3	≤0.0001	2 = 1 > 3	0.0000
Parent, Prt	2	64.3	≤0.0001	1 > 2 = 3	0.0275
FsSt × Age	10	0.85	0.5748	⋯	⋯
Tank × Age	10	13.86	≤0.0001	⋯	⋯
Tank × FsSt	3	3.23	0.0224	⋯	⋯
FsSt × Prt	4	4.51	0.0014	⋯	⋯
Error	378				

Notes: Fused states are: FG = fused groups, colonies that had multiple fusions with two or more others; FP = colonies that had fused with one other colony; and IC = individuals, colonies growing from a single larva.

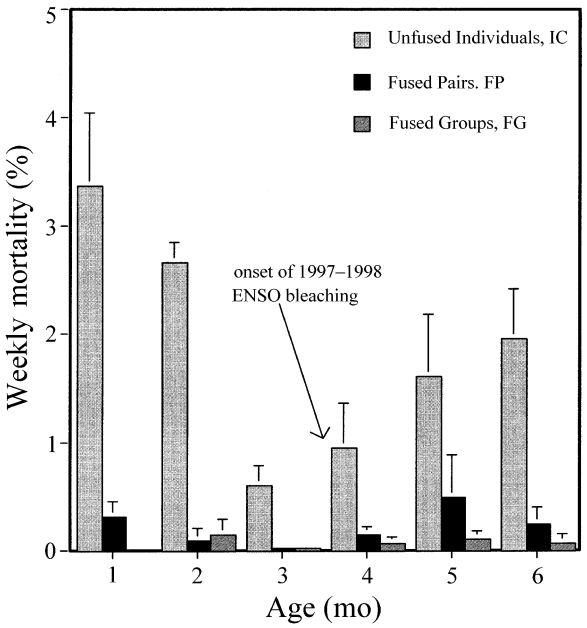

FIG. 3. Weekly percentage mortality of *Pocillopora damicornis* colonies in three fusion group sizes: unfused individual colonies, fused pairs, and fused groups of >2 colonies. Data are means + 1 SE; $n = 3$ rearing tanks.

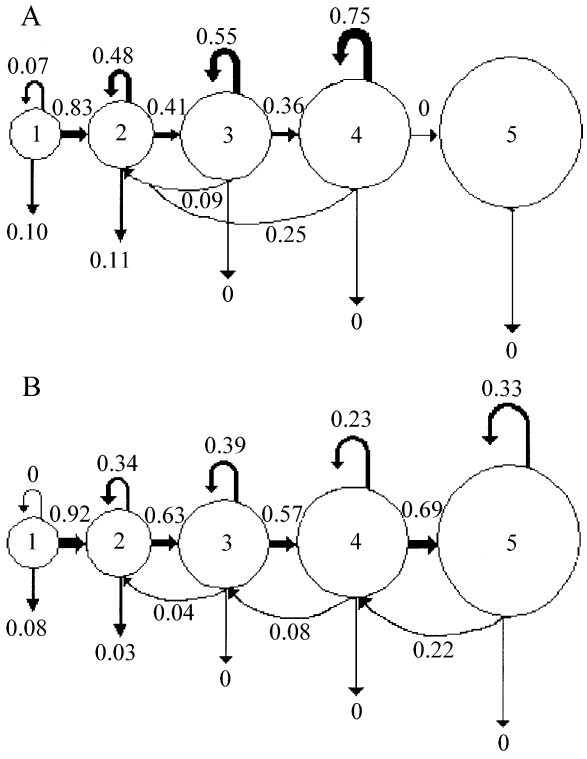

FIG. 4. Transition probabilities for juvenile coral colonies making transitions between size classes: (A) unfused colonies from single settled spat; (B) fused chimeras of two or more colonies. Size class 1 represents size from settlement to 1 mo of age; size class 5 represents the largest size attained after 6 mo of growth.

mained constant (~30%) for chimeras. Analysis of these data revealed that both size class and fused state were significant predictors of colony fate (Table 4). The fused state × size class interaction was not significant, and its removal improved the fit of the model. The effect of size class on fate was inverse (as indicated by the negative *Z* value); as size class increased, its effect on colony fate decreased. This was most likely due to the decrease in numbers of colonies making later transitions, as both death and stasis were high in the smaller size classes. Conversely, fused state directly affected fate, and fused colonies grew faster and underwent stasis less than unfused colonies that stayed within the smaller size classes. Differences in mortality and degrowth between fused and unfused colonies were not significant (Table 4). Therefore, the main effect of fusion in this analysis was an enhancement of growth and transition to the next size class.

Settlement patterns

The dispersion of coral spat on both same-parent ($n = 29$ plates) and mixed-parent ($n = 28$ plates) plates was clearly aggregated. An examination of the test statistic, *c*, calculated per plate, showed that 82.8% of the same-parent plates and 75% of mixed-parent plates had significant *c* values (i.e., >1.96, $\alpha = 0.05$), while 17.2% of same-parent plates and 25% of mixed-parent plates were more uniformly distributed (Fig. 5). Degree of aggregation of juveniles on mixed- vs. same-parent plates did not significantly differ (ANOVA, df = 1,

TABLE 3. Results of logistic regression of group size, parent, and rearing tank on six-month mortality of juvenile coral colonies.

Factor	df	*F*	*P*
Group size	1	12.106	0.0006
Parent	1	21.911	≤0.0001
Tank	1	17.741	≤0.0001
Tank × parent	1	22.672	≤0.0001

TABLE 4. Results of ordinal logistic regression of fused state and size class as predictors of colony fate.

A) General model

Predictor	Parameter estimate coefficient, *Z*	*P*	Odds ratio
Fused state	4.71	<0.0001	34.56
Size class	−4.49	<0.0001	0.53

B) Iterative tests by colony fate

Test	Parameter estimate coefficient	r^2	χ^2	*P*
Mortality	0.68	0.0172	0.979	0.322
Degrowth	0.198	0.001	0.052	0.820
Growth vs. stasis	−1.11	0.49	9.197	0.002

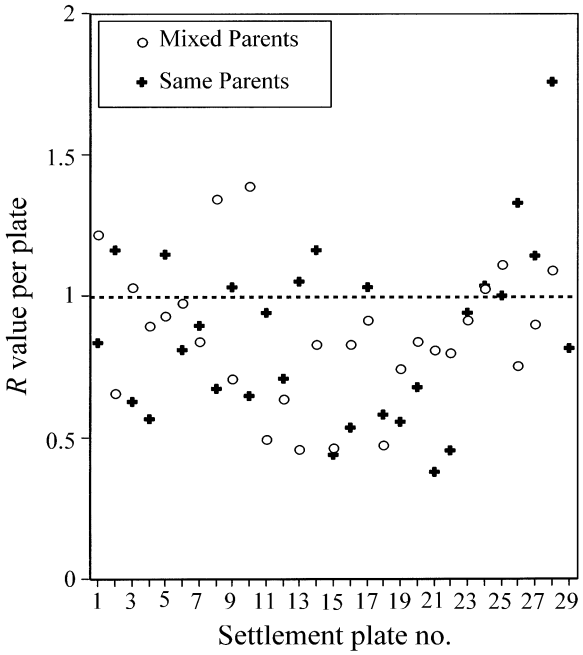

FIG. 5. Degree of aggregation of *Pocillopora damicornis* coral spat on settlement plates of mixed vs. single parentage ($N = 28$ mixed-parent plates and 29 same-parent plates). The dotted line indicates the value of R with completely random distribution; $R > 1$ indicates a uniform distribution, and $R < 1$ indicates a clumped distribution. (For explanation of the degree of randomness, R, see Eq. 1.)

112, $F = 0.0003$, $P = 0.9955$); larvae aggregated equally whether they were in groups of close kin or with unrelated larvae.

DISCUSSION

This study reports on size-dependent demographic traits of the scleractinian coral *Pocillopora damicornis* in the context of coral culture and transplantation. Laboratory settlement and early rearing resulted in significantly greater recruitment, as direct seeding onto reef substrate was largely unsuccessful; only five field-seeded colonies survived to two years out of the 2070 larvae settled in six seeding trials. Post-transplant survival was significantly related to the size of the colony at transplantation, thus supporting a laboratory grow-out stage. Colonies smaller than 1 cm in diameter at transplantation did not become established at the field site, and most died within the first 6 mo. Colony shrinkage after transplantation was much more common among the larger colonies and was probably a response to transplant stress. A number of studies have noted positive correlations between colony or fragment size and survival and/or regeneration (Connell 1973, Bak et al. 1977, Plucer-Rosario and Randall 1987, Harriot and Fisk 1988, Bowden-Kirby 1997), though the reasons were not elucidated. Oren et al. (2001) found a direct correlation between colony size and regenerative capacity in the scleractinian *Favia favus*. Those authors proposed that recovery from injury requires the translocation of energy from colony areas distant to the site of injury. Therefore, the larger the colony (or fragment), the more energy resources available for recovery. In coping with transplant stress, the larger *P. damicornis* juvenile colonies had greater energy reserves that may have afforded a superior chance of recovery. Allocating energy to recovery rather than growth resulted in temporary colony shrinkage in larger colonies, while smaller colonies simply died.

Fusion within the first eight months enhanced survival and growth of colonies. Multiple fusions significantly benefited both growth rate and survival. Mortality was much lower in fused colonies relative to individuals, and lowest among multiple chimeras. Multiple chimeras produced polyps at a faster rate than the other two groups, though the reason for this was unclear. A significant difference in the slopes of the regression lines (Table 2: fused state × age interaction), indicating different growth trajectories, was predicted between fused groups and all others, because of this faster growth rate. The lack of significance in the slopes of the regression lines was likely due to the high variability in growth rate within fused groups, as chimeras ranged from 3 to 10 individuals. However, if larger colonies were producing more polyps because they contained more polyps per colony, an increase in polyp production should be visible as colonies age, regardless of fused state—but this was not visible in our analysis. Our results showed that the rate of polyp production within each group did not significantly change over 6 mo. However, the analysis of growth in the unfused colonies (from the February 1997 cohort) monitored separately (by measuring colony diameter) revealed that weekly growth rate did vary with increasing surface area. Since coral colonies are composed of polyps surrounded by skeleton, growth occurs via both an increase in the number of polyps and skeletal deposition within the coenosteum between polyps. The effect of colony size on growth rate may, therefore, have been manifested in increased skeletal deposition rather than an increase in polyp number. If this was the case, a size-specific growth effect would not have been visible in our polyp counts. A comparison of changes in distances between polyps, polyp production, and colony surface area over time would provide a more discriminating analysis of how size may affect growth rate. Our limited data suggest a mediating effect of fusion on growth that is less straightforward. Growth may be strictly size specific, with fusion simply resulting in larger colonies that grow at rates similar to unfused colonies of comparable size. On the other hand, faster polyp production in multiple chimeras suggests a benefit to multiple fusion that may not operate in either bi-chimeric fusions or individual colonies. In either case, the effect on survival is clearly positive; larger colonies survived better.

The immediate increase in size as a result of fusion is predicted to positively affect growth to reproductive size. Using the transition diagram (Fig. 5) to project future growth, with a mean diameter of 12 mm (63 polyps) at 6 mo, chimeric colonies could reach the documented reproductive size of 4 cm (Holloran 1986) in 1.7 yr. Individual colonies, on the other hand, were an average of 5.5 mm (~35 polyps) at 6 mo. At this rate, colonies would take approximately three years to reach 4 cm. Fusion, therefore, could greatly reduce the length of time to reach a sexually reproductive size, though this should be documented by a longer-term study to follow chimeric vs. individual colonies to reproductive size.

Chimeras formed prior to 8 mo remained stable to 1 yr and grew as single colonies. Although *P. damicornis* is known to produce larvae asexually (Ayre et al. 1997), it is not known how common this is in nature, and given the observed rejection responses, it is unlikely that colonies were from clonally produced larvae. Rejection in colonies contacting after eight months supports the findings of Hidaka (1985) and Hidaka et al. (1997). Those authors found that fusion always occurred in very young colonies and those up to three months between sibling colonies, while colonies from different parents showed either unstable (incompatible) fusion or non-fusion. This suggests similarities in alloimmune maturation between *P. damicornis* and a close relative, *Stylophora pistillata*. *S. pistillata* juveniles showed a four-month maturation period marked by early fusion, followed by transitory fusion and eventual rejection (Frank et al. 1997). Colonies fusing prior to maturation remained stable over time. Our observations of *P. damicornis* suggest a similar pattern, but with a late-onset rejection response (eight months) between close kin (the larvae used here were siblings); close relatives seem to be able to fuse over a longer growth period than can non-kin.

Neither of the documented negative effects observed in ascidians, resorption and parasitism, were observed in our chimeras. Because colony fusion in scleractinians results in a morphologically indistinguishable single colony, such events are not readily observable and have not been documented in corals. It is interesting to note, however, that the greatest benefits occurred in groups of multiple fusions, similar to the findings of Rinkevich (1996). He noted greater colony stability and less resorption in multi-colony chimeras than in bi-chimeric colonies in the ascidian *Botryllus schlosseri* and speculated that the extra-large colonies formed by such aggregations provided superior competitive ability over bi-chimeras and individual colonies.

Larvae settled aggregatively in *P. damicornis*, confirming the findings of Ayre et al. (1997). Gregarious settlement is thought to increase the likelihood of fusion between close kin (Grosberg and Quinn 1986). Although we predicted that larvae from the same parents would aggregate more than those in mixed-parent groups, our trials showed similar aggregation strength. In higher invertebrates, kin aggregation is accomplished by a complex allorecognition system that allows close kin to aggregate, while unrelated larvae settle randomly (Keough 1984). The genetics of recognition in lower invertebrates has not been investigated, but available information suggests a less discriminating system. Larvae of the hydroid *Hydractinia echinata* settle randomly whether with compatible or incompatible larvae, either because they were unable to distinguish kin relationships or because they were unable to alter their initial settlement choice (Yund et al. 1987). Larvae of the sponge *Tedania ignis* do not appear to aggregate or fuse naturally (Maldonado 1998). However, spawning in *Tedania* occurs over a 2-mo period, producing sibling larvae at different times. Forced fusion did not increase survival, though highest mortality was observed 10 d after settlement, suggesting that mortality in *Tedania* juveniles is not strictly size related. Our results suggest two alternative explanations for aggregation patterns in *P. damicornis*: either our assumption that larvae were unrelated is incorrect, or larvae lack the allorecognition ability necessary to distinguish planulae from different parents. *P. damicornis* can produce planulae asexually (Stoddart 1983, Chavez 1986), and if Bantayan reef colonies were doing so, the entire population could be one of very low genetic diversity and high relatedness. Aggregative settlement in mixed groups would be predicted, therefore, because these groups would be closely related or clonal. However, the conditions under which parthenogenesis in *P. damicornis* occurs in nature are unknown, and a sexual mode of reproduction is thought to be more common (Stoddart 1983, Ayre et al. 1997). In addition, rejection between fusing colonies from the same parents at eight months suggested that the larvae produced by the Bantayan reef population were sexually produced. Further, due to the searching behavior larvae undergo prior to settlement, it seems probable that encounters between larvae occurred during the settlement trials, thus providing the opportunity of altering settlement position if a neighbor was recognized as ''non-kin.'' Thus, the most likely explanation for equal aggregation in kin vs. non-kin is that larvae of *P. damicornis* lack allorecognition ability at this stage. On the other hand, larvae could be aggregating on a finer scale than our test could discern without a genetic analysis of the tested population. Such an analysis would provide much more rigorous results for discerning aggregation patterns and should be undertaken as a future step.

Past studies on *P. damicornis* suggest that this species can produce planulae at relatively small sizes. Harrigan (1972) stated that *P. damicornis* is capable of reproduction within one to two years, while Holloran (1986) found planulae in 4-cm-diameter colonies, though colonies smaller than this were not surveyed. In this study, juveniles reared to a minimum of 1-cm

diameter suffered the lowest post-transplantation mortality and had begun spawning within two years (confirmed in July 1999). The new recruits observed on the reef during the one-year census were between 9 mm and 11 mm in diameter, and approximately 8–10 settled juveniles per square meter were observed within the transplant site. Recruit density elsewhere on the reef is difficult to estimate as recruits this size were never seen; adult colonies probably grew from larvae that were cryptically settled. Although Richmond (1987) demonstrated an extended competency period (up to 103 days) in a small percentage of *P. damicornis* larvae, Ayre et al. (1997) discerned inbreeding in Great Barrier Reef populations consistent with local larval recruitment and philopatry. Using the above information regarding philopatry, age at first reproduction, and our observations of aggregative settlement, it is possible that the new recruits observed during the one-year census were products of planula production by the largest transplants starting around one year of age (six months after transplantation). An alternative explanation for the high density of recruits within the transplant sites is that transplants facilitated recruitment and/or survival of juveniles from other sources. Birkeland (1977) noted higher survival of coral recruits in areas with living colonies as compared to areas without living coral, and Clark and Edwards (1995) reported higher mortality of recruits on artificial substrates that did not contain living coral than on those with live coral heads. It seems reasonable to speculate that transplants could have promoted the recruitment we observed, if they were not the direct source of it.

For coral reintroduction to be successful, life-history strategy, demographic traits, and biotic interactions between transplants must be considered. Factors affecting early colony survival (such as larval settlement choice, size-specific mortality, and biotic interactions such as fusion) can influence the structure of the adult population in many coral species (Bak and Engel 1979, Fitzhardinge 1988, Babcock and Mundy 1996). Our present study illustrates that using brooded larvae to create a transplantable coral population is a viable way of introducing such species to degraded reefs. Juveniles were settled and reared in laboratory aquaria with greater success than was obtained by seeding larvae directly onto bare reef substrate. Both size-specific responses (mortality, shrinkage, and growth) and an age-specific response (fusion vs. rejection) significantly affected the performance of coral colonies. In addition, the frequency with which shrinkage occurred increased with colony size in field transplants, suggesting a stress response available only to larger colonies and highlighting the importance of determining an optimum transplant size.

The laboratory protocols developed in this study are applicable to most brooding species. However, the majority of coral species are broadcasters, and modification of these techniques to include the collection of egg/sperm packets, fertilization, and rearing of embryos to a competent larval stage would be needed. As little is known about the reproductive biology of many broadcasting species in the Indo-Pacific (particularly timing and seasonality of spawning), this provides both a challenge and an impetus to increasing the knowledge base for Indo-Pacific corals, particularly species targeted for reintroduction or restoration.

Current opinion regarding the feasibility of mitigating the effects of reef degradation via coral transplants is that it is highly labor intensive, costly, and inefficient in terms of the spatial scale to which it could be reasonably applied (Harriot and Fisk 1988, Edwards and Clark 1998). However, many reefs worldwide continue to decline, showing little or no recovery. This necessitates active rehabilitation and the development of innovative ways to restore reef function. Particularly in areas of extensive habitat loss, such as the Philippines, natural recruitment sources may be lacking. In this study, sexually reproducing transplants were established within two years using brooded larvae settled and cultured in a laboratory facility. Both growth rate and survival were enhanced by chimera formation in laboratory-reared colonies. These approaches suggest a new alternative for reef rehabilitation and coral reintroduction, one that maintains genetic diversity, is nondestructive to donor reefs, and incorporates demographic and life-history traits of cultured species into the culture protocol.

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